

Dipteran parasites and other associates of a communal bee, *Andrena scotica* (Hymenoptera: Apoidea), on Öland, SE Sweden

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Support for and quantification of host-parasite relationships between a facultatively communal, fossorial bee *Andrena scotica* (Hymenoptera: Apoidea) and three Diptera, *Myopa buccata* (Conopidae), *Bombylius major* (Bombyliidae) and *Leucophora personata* (Anthomyiidae), on Öland, SE Sweden, are provided by means of observation of adults at nest entrances of the host bee, dissection of imago hosts and examination of underground brood cells of the host bee. Conopid parasitism was high, with up to 40 % of adult bees at one field site containing one or more conopid larvae. The other two dipteran species were occasional parasites of host brood and pollen provisions. A description of host nest location and entry by *L. personata* and other *Leucophora* species is given when they parasitise a variety of andrenid species. None of the dipteran species have a likely bearing on the evolution or maintenance of communality *per se* in *A. scotica*. Records of other putative parasites and associates of *A. scotica* on Öland are also given.

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Introduction

Andrena is a species-rich genus of ground-nesting (fossorial) bees whose members are a common element of the spring and early summer bee faunas of northern temperate regions of the world (Batra 1990). Of Sweden's 278 indigenous species of bees (Janzon et al. 1991), 54 belong to the genus *Andrena* (Svensson et al. 1990).

Fossorial bees often have numerous organisms associated with them and their nests, some commensal though many others parasitic. For example, a careful study by Batra (1965) revealed 27 species associated with the fossorial bee *Lasioglossum zephyrum* (Hymenoptera: Apoidea) and its nests, many of which were parasitic or damaging. These included Protozoa, Nematoda and mites (Acarina) associated with adult bees; and Diptera, Coleoptera (Meloidae and Rhipiphoridae) and cuckoo bees (Hymenoptera: Apoidea) associated

with host bee larvae. Some of these associations were opportunistic whilst others were more species-specific and appeared to represent close coevolution between host and parasite. Parasites have often been implicated in regulating host bee abundance (Schmid-Hempel & Schmid-Hempel 1989) and, notwithstanding the difficulty in associating a parasite with a fossorial bee host, even in causing the extirpation of populations of fossorial bees (Batra 1966).

Andrena scotica Perkins 1916 (= *Andrena jacobii* Perkins 1921) (Fig. 1) is a fossorial bee, both common and widespread in Europe as far as 62°N (Westrich 1989). It is frequently encountered in urban habitats, too, possibly making it appear more abundant. The species has for long been a focus of investigation at the Ecological Research Station on the island of Öland, SE Sweden



Fig. 1. Two *Andrena scotica* females emerge from a communal nest entrance located between paving stones, Bristol, England. The species is common within urban areas and readily nests between loose stonework overlying soil. Photo: Robert J. Paxton.

Två honor av sandbiet *Andrena scotica* kommer fram ur gemensamt mynningshål beläget mellan stenplattor i Bristol, England. Arten är vanlig bland bebyggelse och anlägger gärna bon under glipor i stenläggningar. Honorna är ungefär lika stora som arbetare av det vanliga honungsbiet.

(ERS, Öland) (Tengö & Bergström 1975, 1977, Tengö 1984). Like many other fossorial bees, a large number of organisms appear to be associated with *A. scotica* and its nests, including many species of Diptera; the latter can be a significant element of the parasites associated with fossorial bees (Batra 1965). Here we provide evidence to support the host-parasite relationship between *A. scotica* and several species of Diptera, and we attempt to quantify their effects on populations of the host bee. We also describe the behaviour of females of anthomyiid flies of the genus *Leucophora* around the nests of the bee, and we give details of other associates of *A. scotica* on Öland.

Material and methods

Study sites, the bee and its dipteran associates

We studied *A. scotica* and its associates at two

field sites, Abbantorp (A) (Fig. 2) and Törnbottnes Stugby (TS) (Fig. 3), circa 12 km apart and both within the Mittlandskogen of Öland (TS: 16°34'E, 56°29'N, 35 m a.s.l.). At both locations, bees constructed fossorial nests into the embankments and raised verges of roads, often utilising abandoned small mammal burrows as nest entrances.

Unlike the majority of *Andrena* species which are solitary nesters, *A. scotica* is facultatively communal. Some females nest alone, though usually two or more - and occasionally hundreds of - females share a single nest entrance (Paxton et al. 1996). Each nestmate female is thought to inhabit her own tunnel beneath the common nest entrance, and to construct her own brood cells within her tunnel and provision them with pollen and nectar that she collects from a wide range of flower species (Westrich 1989). *Andrena scotica*



Fig. 2. Abbantorp, a nesting site for the fossorial bee, *Andrena scotica* on Öland, SE Sweden. At this field site, female bees construct nests within holes in the verges surrounding the road. Photo: Robert J. Paxton.

Abbantorp, boplatz för *Andrena scotica* på Öland. På denna lokal anlägger honorna bon i befintliga hål i väggkanterna.

is considered univoltine and, at our field sites on Öland, adults were active from mid-May to the beginning of July. Offspring are thought to complete their development in their natal cells and first emerge the following spring from their natal nest entrance.

Three species of Diptera, *Myopa buccata* (Linnaeus 1758)(Conopidae), *Bombylius major* Linnaeus 1758 (Bombyliidae) and *Leucophora personata* (Collin 1921) (Anthomyiidae), were observed at or near the nest entrances of *A. scotica* on Öland or around flowers upon which *A. scotica* females were foraging; they are likely parasites of this bee.

Support for and quantification of parasitism by Diptera

A variety of methods was employed to quantify the rates of parasitism of *A. scotica* by its putative



Fig. 3. An artificial nesting tube for *Andrena scotica*, comprising a drainage pipe filled with soil, is being buried at field site TS, Öland, SE Sweden, by one of the authors (RJP) in March 1995, immediately preceding the flight season of the bee; other tubes await burial. Photo: Robert J. Paxton.

Artificiellt borör för *Andrena scotica* gjort av plaströr fyllt med jord, grävs ner vid Törnbottens Stugby på Öland av en av författarna (RJP) i mars 1995, före biets flygperiod. Andra rör ligger i väntan på att bli nergrävda.

parasitic Diptera. During the flight season of 1993, adult female bees were collected as they returned to their nest entrances at A and TS carrying pollen in the 'scopal' hairs of their rear legs and mesosoma; the pollen is used to provision brood cells. Thus all sampled bees were presumably reproductively active. Bees were immediately frozen, subsequently dissected under insect saline (0.9% NaCl solution) and examined using a binocular microscope (x 40 magnification) for the presence of conopid eggs or larvae, a reliable method of detection (Schmid-Hempel & Schmid-Hempel 1996). To determine whether host bees were reproductively active, the number and size of oocytes in their ovarioles were recorded. Also, each bee's spermatheca was removed and examined using phase contrast microscopy (x 400 magnification) for the presence of spermatozoa as an indication of whether or not she had mated.

Nest entrances at A and TS to which female bees returned carrying pollen during the flight season of 1993 were permanently marked with metal and plastic tags. Field site A comprised 15 nests in an area of 7.2 m x 36.5 m. Field site TS comprised 38 nests in an area of 7.5 m x 330.0 m. The number of *A. scotica* nestmate females using many of the nest entrances at TS in 1993 was estimated by mark-recapture during the height of the flight season (see Paxton et al. 1996 for details). At the beginning of May 1994, before the emergence of any bees, 'emergence traps', comprising nylon netting supported by a wire frame (see Paxton & Tengö 1996 for details), were placed over 17 nest entrances at TS to collect all offspring and parasites that were to emerge from those nests during the 1994 flight season of the bee. *A. scotica* was the only non-parasitic bee species to be caught in the emergence traps, suggesting that no other potential host species utilized the same entrances as fossorial nests. Nets were removed at the end of the flight season in 1994 and then replaced over a sample of the same nest entrances for the following two flight seasons. Emergence traps were inspected at least twice per day across the entire flight seasons of *A. scotica*, and all organisms caught therein were removed, weighed on an analytical benchtop balance (± 0.1 mg) and identified.

Natural nests of *A. scotica* are difficult to excavate at field sites A and TS because they lie

beneath large boulders and, often, several decimetres of Swedish asphalt. To allow easier excavation of nests, in March 1995 we employed artificial nesting tubes for *A. scotica* at TS by filling plastic drainage pipes (15 cm diameter, 60 cm length) with soil and burying them into the road embankments (Fig. 3). *Andrena scotica* females that had freshly emerged from nests into emergence traps at TS were marked individually on their thoraces with paint and kept overnight in a refrigerator (+4°C). The next morning, the chilled bees were carefully placed at the bottom of 25 cm long tunnels which we had dug into the soil filling each of these artificial nesting tubes. The bees emerged from the tubes and subsequently utilised them for constructing and provisioning their cells. In March 1996, two of these artificial nesting tubes, which had been utilised by three and six females respectively, were removed from TS and excavated in the laboratory to determine the number and contents of *A. scotica* brood cells that had been constructed therein during the 1995 flight season of the bee.

Occasional observations were made at field sites A and TS of the bees and their parasites during the host's flight seasons from 1993 to 1996, involving both behavioural observation of adults and dissection of adults and examination of their internal tissues by light microscopy. Within-nest observations were also made during the 1996 flight season through the use of artificial nesting tubes positioned within a subterranean outhouse illuminated with red light at the ERS, Öland. Freshly emerged bees from TS were again individually marked and released into soil-filled metal nesting tubes (diameter 25 cm, length 60 cm), overlain with a sheet of perspex to allow intranidal observation. These bees utilised the tubes for constructing and provisioning their brood cells, gaining access to the outside via plastic tubing (14 mm diameter) which ran from the top of each nesting tube, through the wall of the outhouse and to the soil surface outside.

Results

Conopidae

In total, 240 *A. scotica* adult females were collected as they returned to their nests at A and TS carrying pollen provisions in their scopal hairs. Females returning to their nests all

Tab. 1. Rates of conopid parasitism of adult *Andrena scotica* females (returning to their nests with pollen provisions) at two field sites, A and TS, on Öland, SE Sweden.

Grad av parasitering av stekelflugor (conopider) på vuxna honor av sandbiet *Andrena scotica* (återvändande till sina bon med pollenproviant) vid två undersökta lokaler, A och TS på Öland.

Site	Date	Number of females (hosts) examined	Number of females (hosts) containing ≥ 1 conopid
A	930603	60	2 (3.3 %)
TS	930607	120	15 (12.5 %)
TS	930613	20	8 (40.0 %)
A	930622	20	4 (20.0 %)
TS	930622	20	4 (20.0 %)
TOTAL		240	33 (13.8 %)

contained pollen and nectar in their crops and pollen husks in their recta, the contents of the crop possibly being used to supplement the pollen being transported in the scopal hairs as brood cell provisions. Conopid eggs and larvae were readily detected within the gasters of host bees, the eggs being anchored to fat tissue within the haemocoels of hosts by their terminal hooks (Fig. 4). Eggs were those of a *Myopa* species (Smith & Peterson 1987, and see Fig. 4). Larvae were most likely those of *Myopa*, but no published key currently exists with which to distinguish *Myopa* larvae from those of other conopids.

Conopid parasitism of *A. scotica* females varied from 3.3 % to 40.0 % per field site, depending upon date of collection and site (Tab. 1), with one host female containing 2 conopid larvae and the others each containing one conopid egg or larva. Seven of 240 female bees (2.9 %) had undeveloped or regressed ovaries that did not contain an enlarged oocyte whereas all other bees examined contained one or more (maximum 4) enlarged oocytes within their ovarioles. Of the 162 *A. scotica* spermathecae that were successfully examined, 5 (3.1 %) did not contain spermatozoa.

Parasitism by conopid eggs and larvae was significantly associated with a lack of oocyte development (Fisher's exact test $P = 0.008$), but absence of spermatozoa in the spermathecae of host bees was not associated with conopid parasitism (Fisher's exact test $P = 0.148$). Interestingly, one female bee returning to a nest with pollen provisions had neither enlarged oocytes nor spermatozoa, though it did contain a well-developed conopid larva in its haemocoel.

Two species of Conopidae were caught within emergence traps at TS during the flight season of 1994 as they emerged from *A. scotica* nest

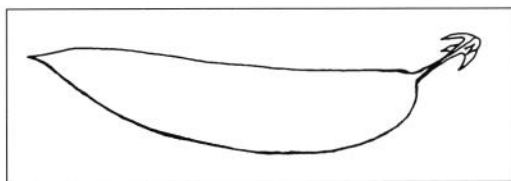


Fig. 4. An egg of *Myopa buccata* (after Smith & Peterson 1987), showing the terminal anchor-like process that presumably secures the egg to host tissue within the host's gaster. Total length: 1.2 mm.

Ägg av stekelflugan *Myopa buccata* med terminalt ankarutskott som antagligen fäster ägget i någon vävnad inom värdens bakkropp.

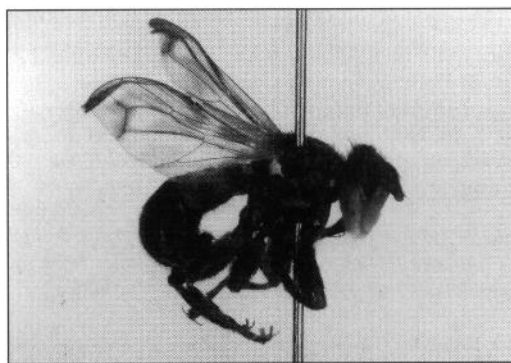


Fig. 5. The conopid fly *Myopa buccata*, a common parasite of adult female *Andrena scotica* on Öland, SE Sweden. Larvae of the fly develop within the gaster of the host bee. Photo: Rune Axelsson.

Stekelflugan *Myopa buccata* tycks vara en allmän parasit på honor av *Andrena scotica* på Öland. Dess larver utvecklas inuti bakkroppen hos värdbiet.

entrances, *Myopa buccata* (Fig. 5) and *Myopa testacea* (Linnaeus 1759) (Tab. 2). It is most likely that their putative parasitised hosts, *A. scotica* females, died within the nests in which they were provisioning cells and that the conopid pupae subsequently overwintered *in situ* within the hosts' nests before emerging the following spring. This view is supported by the fact that there was a significant positive relationship between the number of *M. buccata* adults emerging from nests into emergence traps at TS in 1994 and the number of putative host nestmate females using those nests in the 1993 flight season (Fig. 6).

Myopa buccata, the commonest British conopid (Smith 1959), was by far the most frequent conopid recorded in the emergence traps (Tab. 2), and it is also the most frequently recorded and widely distributed of Sweden's spring conopids. It is most likely the commonest conopid parasite of *A. scotica* adults at TS. The size (weight) of emerging *M. buccata*, at 37.6 ± 3.9 mg (mean \pm standard error), was less than that of *A. scotica* females at emergence (71.1 ± 0.4 mg), in accordance with the suggestion that it is a parasite of *A. scotica*. There was no difference between male and female *M. buccata* in their weights at emergence (Mann Whitney U = 18.00, $n_1 = 9$, $n_2 = 7$, n.s.) nor in their dates of emergence (Mann Whitney U = 31.50, $n_1 = 9$, $n_2 = 7$, n.s.), but *M. buccata* adults emerged significantly earlier in the year than their putative host females (Mann Whitney U = 132.00, $n_1 = 489$, $n_2 = 16$, $P < 0.001$;

Tab. 2. Diptera emerging from *Andrena scotica* nests at field site TS, Öland, SE Sweden, during 1994-96, and which are putative parasites of the bee, with dates of capture in emergence traps shown in parentheses.

Flugor (förmodade parasiter till biet) kläckta från bon av *Andrena scotica* vid lokal TS, Öland, under 1994-96, med fångstdatum i kläckningsfällor inom parantes.

Species (Family)	1994		1995		1996	
	Females	Males	Females	Males	Females	Males
<i>Myopa buccata</i> (Conopidae)	9 (Fig. 7)	7 (Fig. 7)	1 (950521)		1 (960611)	
<i>Myopa testacea</i> (Conopidae)	1 (940508)	1 (940517)				
<i>Leucophora personata</i> (Anthomyiidae)	1 (940622)	1 (940504)	3 (950512) (950516) (950516)			

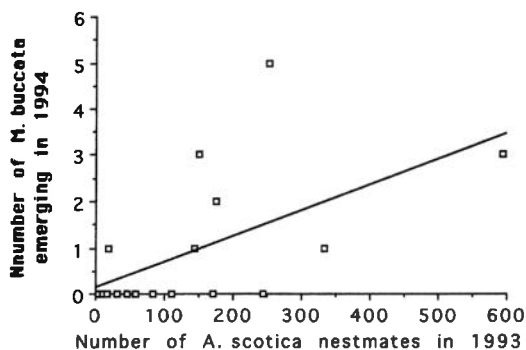


Fig. 6. The number of *Myopa buccata* adults emerging from nests of *Andrena scotica* at field site TS, Öland, SE Sweden, in 1994 is plotted upon the number of *A. scotica* females estimated to have been using those nests during the preceding flight season, spring 1993. The regression line is shown, where $y = 0.138 + 0.006x$, ANOVA of regression $F_{1,15} = 7.208$, $P < 0.05$.

Antal imagines av *Myopa buccata* kläckta från bon av *Andrena scotica* på lokal TS, Öland, 1994 i relation till antalet *A. scotica* honor som skattas ha använt dessa bon under föregående flygsäsong, våren 1993.

Fig. 7) by approximately 20 days at TS in 1994.

Two *Myopa* adults emerged over subsequent years, flight seasons 1995 and 1996, into emergence traps at TS (Tab. 2). Either *Myopa* has a lifecycle in which some offspring delay their emergence until they have passed more than one winter in development (i.e. some individuals of an age cohort require an additional year or more to complete development, termed 'parsivoltinism') or closely adjacent nests of *A. scotica* are interconnected below ground. Parsivoltinism may also be exhibited by *A. scotica* and its other putative parasites at TS, too. However, more conclusive evidence than that provided by emergence traps should be sought to confirm this suggestion.

Conclusive evidence for the *A. scotica*-*Myopa* parasitic relationship comes from the excavation of one of the artificial nesting tubes at TS which *A. scotica* female imagines used in 1995 to provision offspring (Tab. 3). A *Myopa* puparium with a female ready to hatch was found between the gastral sterna and terga of an *A. scotica* female who had died within the entrance of artificial nesting tube F, possibly a bee who had provisioned brood cells within the tube during 1995.

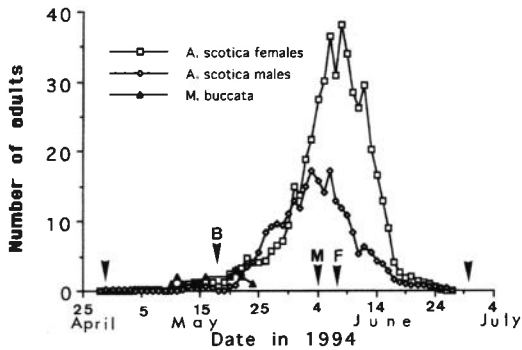


Fig. 7. The pattern of emergence in 1994 of *Myopa buccata* adults from *Andrena scotica* nests at field site TS, Öland, SE Sweden, and that of *A. scotica* in the same year from one typical nest, S7, at the same location (Paxton & Tengö 1996). For *A. scotica*, the pattern shows the 5-day averaged schedule of emergence. Arrows indicate the start and end of observations and the median date of emergence of *M. buccata* (B, 940518) and female and male *A. scotica* (female: F, 940607; male: M, 940604).

Kläckningsmönster 1994 för imagines av *Myopa buccata* från bon av *Andrena scotica* på lokal TS, Öland, och för *A. scotica* från ett typiskt bo (S7) på samma lokal (se Paxton & Tengö 1996). För *A. scotica* visar mönstret den genomsnittliga 5-dagarsperioden av kläckning. Pilar utmärker observationstidens början och slut samt mediandatum för kläckningar av *M. buccata* (B, 940518) och honor och hanar av *A. jacobi* (honor: F, 940607; hanar: M, 940604).

Bombyliidae

Bombylius major was the only bombyliid parasitic on bees that was recorded at TS, where it was often observed during the flight season of *A. scotica*. Females of *B. major* flew slowly along the embankments of field site TS, between 10 and 20 cm above the soil surface, hovering above openings in the ground, including nest entrances of *A. scotica*. They oviposited in flight by flicking eggs from the tip of the abdomen into openings in the ground (cf. Andrietti et al. 1997).

Excavation of artificial nesting tubes D and F from field site TS in March 1996, in which 3 and 6 *A. scotica* females respectively had provisioned offspring in 1995, revealed a total of 3 *Bombylius* larvae within otherwise empty host brood cells (Tab. 3). All other host brood cells contained hibernating host imago offspring, mouldy pollen or, in one instance, an empty cell with an

Tab. 3. Contents of *Andrena scotica* brood cells associated with nests in two artificial nesting tubes. Nests were provisioned by host females at field site TS, Öland, SE Sweden, in the spring of 1995 and were subsequently excavated on the 18th and 19th March 1996. Nest D was provisioned by 3 females and nest F by 6 females.

Innehåll i yngelceller av *Andrena scotica* i två artificiella borör. Bona provianterades av värdhonor vid lokal TS, Öland, under våren 1995 och grävdes därefter upp 18-19.3 1996. Bo D provianterades av tre honor och bo F av sex honor.

Contents of brood cells	Nest D	Nest F
<i>Andrena scotica</i>	10 female adults 9 male adults	12 female adults 6 male adults
<i>Bombylius</i>	1 larva	2 larvae
<i>Leucophora personata</i>	1 puparium (adjacent to cell)	0
mouldy pollen	0	8 brood cells
Conopidae*	0	1 puparium

* conopid puparium found between sclera and terga of an adult female *A. scotica* within the main tunnel of the nest and not associated with a brood cell.

associated *Leucophora* puparium (Tab. 3). Under the assumption that a *Bombylius* (or *Leucophora*) larva consumes the contents of one host cell, the average rate of parasitism by *Bombylius* of *A. scotica* at TS was 6.1 % in 1995 (Tab. 4).

Following excavation of *Bombylius* larvae in March 1996 from artificial nesting tubes, they were kept at field temperatures, but they only developed as far as pupae within exuvia before becoming quiescent. This suggests that they require two or more winters to complete development.

Anthomyiidae

Females of *Leucophora personata*, previously recorded from Skåne (Hennig 1976), were occasionally noted at natural nest sites of *A. scotica* on Öland. They often sat on vantage points overlooking nest entrances and flew towards and pursued passing insects, including *A. scotica* females returning to their nests carrying pollen. A pursuing *L. personata* always followed 5-10 cm behind a bee. These observations corroborate others describing this and other *Leucophora* species 'shadowing' a range of host bee species (Huie

1916, Collin 1920, Copeman 1921, Davis & Laberge 1975, Schrader & Laberge 1978, Meyer-Holzappel 1986). In Britain, *L. personata*'s putative hosts are *Andrena labialis*, *Andrena nigroaenea* and *Andrena trimmerana* (Collin 1920), the latter being closely related to *A. scotica*.

Observations outside the entrances of the artificial nesting tubes at the ERS, Öland, suggested that a female *A. scotica* returning to its nest with pollen provisions and that was pursued by a *L. personata* did not enter its nest directly, as was usually the case, but rather flew away, to return some minutes later to attempt to re-enter its nest. This apparent evasion of *Leucophora* parasites may be widespread among fossorial bees (e.g. Batra 1965, Knerer & Atwood 1967). *Leucophora personata* females who successfully located an *A. scotica* nest entrance spent over 20 minutes walking within the labyrinth of small tunnels that existed behind the main entrance shaft to the observation nests.

Leucophora personata adults were caught in the emergence traps above *A. scotica* nest entrances at TS (Tab. 2), supporting the notion that this anthomyiid fly is a parasite of *A. scotica*. The timing of emergence of *L. personata* adults from *A. scotica* nest entrances during the period of emergence and provisioning of the bee gives these Diptera ample opportunity to act as parasites of *A. scotica* (Tab. 2 and Fig. 7). However, numbers of emerging *L. personata* caught in emergence traps were low (Tab. 2); two *L. personata* adults emerged into traps at TS in 1994 as compared to over 8 900 *A. scotica*, suggesting that this dipteran rarely parasitises *A. scotica* cell contents. Some other *Leucophora* are far more successful at parasitising their solitary, fossorial host bees (Eickwort et al. 1996).

Three *L. personata* adults were found in emergence traps over *A. scotica* nest entrances in the second year of their use at TS (Tab. 2). As for the conopids, this may reflect the fact that some *L. personata* exhibit a parsivoltine lifecycle or that closely adjacent nests of *A. scotica* are interconnected below ground.

Excavation of *A. scotica* nests constructed into artificial nesting tubes D and F at TS revealed one *L. personata* male imago within its puparium and located 5 mm away from a sealed yet empty *A. scotica* brood cell, with a narrow burrow leading

from the cell to the puparium. This provides further support for *L. personata* being a parasite of *A. scotica* at TS.

In Hennig's (1976) key, the female specimens of *L. personata* from TS rather run to *L. obtusa*, which is said to differ in having its first sternum hairy. Clearly, though, at least the TS population of *L. personata* has this sternum quite hairy. Females of the two species differ in several other characters. The pre-alar bristle is as long as the dorsocentrals in *L. personata*, less than half as long in *L. obtusa*. *Leucophora personata* has at most a vague darker middle stripe on the mesonotum and an incomplete brown middle stripe on the terga (covering on the 5th tergum only the basal third of its length), both these stripes being strongly marked in *L. obtusa*. The wing veins are more yellowish in *L. personata* and the posterior cross-vein is more oblique and S-curved.

Other associates

Insect parasites and pests other than Diptera that we have associated with *A. scotica* at field sites A and TS include *Nomada marshalli* (Kirby 1802) (Hymenoptera: Apoidea), *Meloe violaceus* Marsham 1802 (Coleoptera: Meloidae) and a strepsipteran. *N. marshalli*, a known cuckoo bee brood parasite of *A. scotica* throughout the host species' range in N and C Europe (Westrich 1989), destroyed approximately 8.4 % of host offspring that were provisioned at TS in 1993 (Tengö & Paxton in prep.).

Adults of *M. violaceus* were often seen in April and May, crawling across field sites, and their triungulin larvae were regularly encountered on the tops of flowers in bloom. Meloid triungulins attach themselves to flower-visiting bees to be transported back to host nests, where they move from host imago to host brood cell in order to feed upon cell contents (Pinto & Selander 1970). Though we never saw triungulins on *A. scotica* females at A or TS, it is unlikely that we would have found them given meloids' life history. This is because all triungulins would be expected to move from host female to host female's brood cell whenever the host female returned to her nest. Male bees do not provision brood cells and rarely return to nests. Therefore meloid triungulins that attach themselves to male bees stand more chance of being detected. Indeed, of 28 male *A. scotica* sampled at and around A and TS in 1993, 57 % (n

= 16 of 28 males) had one or more *Meloe* triungulins attached to their thoraces. One male *A. scotica* was found at TS in 1994 with 515 triungulins adhering to it. With so many triungulins attached, it could not fly, and only with difficulty was it able to crawl across the ground. *Meloe violaceus* is thought to be a parasite of numerous fossorial bees (Westrich 1989), and it is a potential parasite of *A. scotica* at TS.

Strepsiptera are internal parasites of aculeate Hymenoptera and other insects (Askew 1971) and have been recorded from *A. scotica* in Britain (RJP pers. obs.) and at field site TS (JT pers. obs.). However, our inspection of several thousands of imago *A. scotica* at A and TS from 1993 to 1996 did not reveal any to be parasitised by Strepsiptera.

Numerous nematodes have been associated with fossorial bees (Giblin-Davis et al. 1990) and, in this regard, *A. scotica* on Öland is no exception. Mermithid nematodes, generalist parasites of soil-dwelling and aquatic invertebrates (Buxton 1989), were seen within the haemocoel of one emerging *A. scotica* female imago at TS in 1995, but we have otherwise not recorded their presence despite the examination of several hundreds of individuals. They are undoubtedly of minor importance to this bee on Öland. However, many *A. scotica* females carried dauer juvenile stages of another, currently undescribed, diplogasterid nematode (C. Erteld 1995 pers. comm.) within the intersegmental glands of their haemocoels. Related nematodes are frequently encountered in fossorial bees, both solitary and social (Giblin-Davis et al. 1990), and they have been hypothesised to be of benefit to host bees by consuming bacteria and fungi in host cells (Erteld 1995). A microsporidium (Protozoa: Microsporidia) was also associated with *A. scotica* adults on Öland, infecting the fat bodies of all adults at TS in 1995 (Paxton et al. 1997). This newly described microorganism (Fries et al. in prep.) had a negative effect on host female fecundity (Paxton et al. 1997). Other microsporidia are well-characterised debilitating intracellular parasites of animals, including bees (Macfarlane et al. 1995).

Finally, it may be worth mentioning that among the more accidental fly species captured in the emergence traps at TS in 1995 were two males and one female of *Phyto melanocephala* (Meigen 1824) (Rhinophoridae). This species has been

reported only once before from Scandinavia, from Skåne (Hedström 1988). It is a parasitoid of woodlice (Isopoda: Oniscoidea) and cannot be imagined to have any direct relation to *A. scotica*.

Discussion

We have associated a diversity of organisms with *A. scotica* at our two field sites on Öland with varying degrees of confidence. These associates differed in their abundance and putative effects on host bees (Tab. 4), and undoubtedly their impact on host bee populations also changes across years with variation in their abundance.

Conopidae

Adult female conopids lay eggs into the gasters of hosts, usually adult aculeate Hymenoptera, and they are often not host-species specific (Smith 1959). Larvae develop by consuming host haemolymph and subsequently host internal organs (Schmid-Hempel & Schmid-Hempel 1996). A parasitised host soon dies (circa 10 days for conopids parasitising bumble bee workers, Schmid-Hempel & Schmid-Hempel 1996), whereupon the conopid pupates and, for temperate species, overwinters within the host's gaster before emerging the following spring (Schmid-Hempel & Schmid-Hempel 1988).

For *Andrena accepta*, a North American communal bee, Rozen (1973) has shown that conopid parasitism is associated with loss of ovarian development of the host. Our data suggest that the same is true for *A. scotica* parasitised by *Myopa*. However, most *A. scotica* females that contained a *Myopa* egg or larva still had mature oocytes, suggesting that loss of fertility occurs rather late following *Myopa* parasitism, of obvious advantage to the host.

It has been clearly demonstrated that bumble bee workers containing a conopid larva often burrow beneath the soil surface immediately prior to death by conopid parasitism, enhancing conopid fitness (Müller 1994a); this manipulation of host behaviour has therefore been interpreted as adaptive on the part of the conopid (Müller 1994b). Similar parasite modification of host behaviour may also occur in the *A. scotica*-*M. buccata* association. *Andrena scotica* females parasitised by a *M. buccata* larva may return to their nest to die, hence the emergence of conopid

Tab. 4. Summary information on the organisms associated with *Andrena scotica* at two field sites, A and TS, on Öland, SE Sweden, their putative effects on host bees, and their maximal recorded abundance in 1993-96 as a percentage of hosts infected.

Organismer associerade till sandbiet *Andrena scotica* vid två lokaler på Öland, A och TS, deras förmodade effekt på värdbin samt deras maximalt noterade abundans under 1993-96, uttryckt som % infekterade värdbin.

Associated organism	Stage of host affected	Effect on host	Abundance (% hosts infected)	Source of data
<i>Myopa buccata</i>	adult	death	40.0 %	Dissection of adults
<i>Bombylius major</i>	larva/pupa	death	6.1 %	Excavation of nests
<i>Leucophora personata</i>	larva/larval food	death	2.0 %	Excavation of nests
<i>Nomada marshamella</i>	larva/larval food	death	8.4 %	Emergence nets
<i>Meloe violaceus</i>	larva/pupa	death	(low ?)	Excavation of nests
Strepsiptera	adult	zero fecundity	not observed	Visual examination and dissection of adults
mermithid nematode	adult	(negative ?)	low	Dissection of adults
diplogasterid nematode	adult	(positive ?)	high	Dissection of adults
microsporidium	adult	reduced fecundity	100 %	Dissection of adults

flies the following spring from the nest entrances of *A. scotica*.

Temporal synchrony between host and parasite is thought to benefit the parasite, though relevant data on bee host-parasite synchrony are equivocal (Wcislo et al. 1994). Ascertaining whether schedules of emergence for *A. scotica*-*M. buccata* are adaptive on the part of the conopid requires knowledge of the longevity of imago conopids and the duration of adult development required for them to reach maturity after emerging from a puparium in spring, information which is currently lacking. Further, *M. buccata* parasitises other spring bee species (Smith 1959, Maeta & Macfarlane 1993). *A. scotica* may not be its principal host at field site TS, and thus synchrony with *A. scotica* may be of little relevance to the evolution of *M. buccata*'s schedule of emergence on Öland.

Parasitism of adult bumble bees by conopids has recently been demonstrated to be high (Schmid-Hempel & Schmid-Hempel 1988, Schmid-Hempel et al. 1990), and more frequent than might be assumed from the number of conopids in insect collections (Maeta & Macfarlane 1993). There is a high frequency of parasitism by conopids of *A. scotica* during at least some periods of the host's flight season, too. This suggests that *M. buccata*

could act as a regulator of host abundance, as has been implicated for other conopids parasitising bumble bees (Schmid-Hempel & Schmid-Hempel 1989). Given the rapid development of conopid larvae, and thus rapid host death following parasitism (Schmid-Hempel & Schmid-Hempel 1996), it is most likely that parasitism of adult *A. scotica* by conopids is even higher than that suggested by our data (Tab. 4).

Bombyliidae

Bee flies (Bombyliidae) are common parasites of fossorial bees (Packer 1988, Westrich 1989). Adult female bee flies cover their eggs with fine particles of soil which they have previously collected in a 'dust basket' under the tip of the abdomen (Stubbs 1997). They then oviposit in flight by flicking dust-covered eggs into host nests in a distinctive fashion, hovering above a nest entrance or other opening in the soil surface and ovipositing with a characteristic bobbing motion of the abdomen (Andrietti et al. 1996). Bee fly first instar larvae (planidia) crawl through the soil to a host cell, where they sit upon the host larva, awaiting further development of the host. The bee fly larva then consumes the host larva before burrowing away from the host cell to meta-

morphose in a self-constructed cavity at some distance from the host cell (Bohart et al. 1960). Many host-parasite relationships among bee flies are uncertain (Stubbs 1997), but it seems that many bee fly species, including the common N and C European *B. major*, parasitise a large number of host bee species (Askew 1971); *B. major* is most likely a parasite of *A. scotica* at field site TS.

If parasitism by *Bombylius* was frequent at TS, as excavations of host nests in artificial nesting tubes suggested, it is paradoxical that adults of *Bombylius* were not caught in emergence traps (Tab. 2). *Bombylius* larvae have large spines, proximally and distally, and burrow away from host brood cells after consuming the host larva or pupa (Bohart et al. 1960), emerging above ground not through the host's natal tunnel but rather through their own self-constructed tunnels. They were therefore unlikely to have been caught by our emergence traps at TS.

Our evidence suggests that *Bombylius* requires more than one whole year to complete development from egg to adult when parasitising *A. scotica*. Similarly, *B. major* larvae parasitising *Andrena fulva* (Müller, 1776) in Britain appear to require two years to complete development (RJP pers. obs.). Batra's (1965) observations of *Bombylius pulchellus* parasitising the bee *L. zephyrum* are also of relevance; though bombyliid exuvia could be excavated from around host bee cells, their diapause could not be broken in their first year of development (Batra 1965). A two-year or multi-year lifecycle may be a widespread feature of temperate bombyliids (Bohart et al. 1960), whose larvae are able to slow down or stop their own development and wait until host larvae have grown large before commencing to feed on hosts (Packer 1988).

Anthomyiidae

Anthomyiid flies of the genus *Leucophora* have occasionally been recorded as putative parasites of fossorial bees (e.g. Huie 1916, Copeman 1921), though little is known of the biology of this group of Diptera. Adult flies follow host female bees laden with pollen to their nests, pursuing the bee in flight at a fixed distance (Schrader & Laberge 1978). After locating the host's nest entrance, flies enter the host nest to oviposit. *Leucophora* larvae apparently consume the pollen provisions of the



Fig. 8. A female of the anthomyiid fly *Leucophora obtusa* enters an *Andrena fulva* tunnel head-first, possibly to inspect its contents, in Cardiff, Wales. Photo: Robert J. Paxton.

En hona av blomsterflugan *Leucophora obtusa* tränger in i en bogång av sandbiet *Andrena fulva* i Cardiff, Wales, troligen för att undersöka dess innehåll.

host's larva (Collin 1920) and, possibly, the host larva too (Batra 1965). They then burrow a short distance from the host's brood cell to pupate (Davis & Laberge 1975). They are apparently not host-specific (Meyer-Holzappel 1986).

Observations of *Leucophora obtusa* (Zetterstedt 1838) parasitising the solitary fossorial bees *Andrena fulva* and *Andrena nitida* (Müller 1776) (= *Andrena pubescens* Olivier 1789) in Cardiff, Wales, have shown that, after locating a host nest into which a host female had entered with pollen provisions, a *L. obtusa* female usually waited for the host to subsequently depart from her nest before entering the nest head-first for up to 2 minutes (Fig. 8). Thereafter, the fly reversed out of the tunnel and then either flew away to a vantage point to seek another potential host or it turned around and re-entered the host nest abdomen-first for a period of up to 10 minutes, presumably to oviposit (RJP pers. obs.). Identical behaviour, in which a female *Leucophora* awaits the departure of its host bee before entering the host's nest, has been recorded for *L. obtusa*

parasitising *Andrena regularis* in the USA (Schrader & Laberge 1978) and *Leucophora grisea* parasitising *Andrena tarsata* in Scotland (Huie 1916) and parasitising the fossorial andrenid bee *Panurgus banksianus* in Switzerland (Meyer-Holzapfel 1986). Contrarily, Copeman (1921) and Davis & Laberge (1975) recorded *L. obtusa* directly entering host nests, whilst hosts were still within their nests, in pursuit of their hosts. *A. fulva* in London and *Andrena erigeniae* in the USA respectively. *L. obtusa* has also been reported to oviposit directly at the entrance to fossorial nests of *Andrena bipunctata* in America (Michener & Rettenmeyer 1956). Our observations of *L. personata* parasitising *A. scotica* suggest that flies enter in pursuit of host females returning to their nests with pollen. Differences in host nest architecture may partly underlie intra- and interspecific variation in *Leucophora* parasitic behaviour.

What is less clear is where *Leucophora* females oviposit, and the means by which their larvae reach host brood cells (Schrader & Laberge 1978). Our above- and below-ground observations at the ERS, Öland, indicate that *L. personata* females spend some time within host nests, possibly searching for cells currently being provisioned and in or near which to oviposit.

The host Andrena scotica, communal nesting and parasitism

Bee species vary in the stage at which they diapause, with many temperate species that have a flight season during spring thought to overwinter as diapausing adults, and those with a summer or autumn flight season thought to overwinter as prepupae (Westrich 1989). Our excavations of nests in March 1996 that had been provisioned in 1995 within artificial nesting tubes confirms that *A. scotica* overwinters as fully developed adults within their natal brood cells, those cells still closed since having been sealed from the outside by their mothers directly after their mass provisioning the previous spring. Bees only first exit their natal brood cells in spring, prior to emergence from their natal tunnel. This observation is of relevance to the mating system of *A. scotica*, in which a high proportion of females mate within their nest (intranidally) (Paxton & Tengö 1996). Clearly, intranidal mating must occur in spring, before first emergence of adults above ground, rather than in the previous autumn.

Defence against parasites that the sharing of a common nest entrance affords has been hypothesised to be a major selective factor favouring the evolution of sociality in insects (Lin & Michener 1972). However, the frequency of brood parasitism by Diptera appears to be too low (Tab. 4) to provide a sufficient selective force favouring communal nesting in *A. scotica*. Conopid parasitism of adult *A. scotica*, on the other hand, seems to be rather frequent (Tab. 4). Conopids are thought to parasitise adult hosts at flowers and away from host nests (Smith & Peterson 1987). Indeed, we have only observed freshly emerged (teneral) *Myopa* at nest entrances, presumably immediately following their emergence from overwintering inside host nests, and never actively searching for hosts at nest entrances. In addition, there was no relationship between the proportion of conopid-parasitised hosts and the number of nestmates for *A. scotica* females returning to nests at TS in 1993 (Spearman rank correlation, $r_s = -0.086$, $n = 8$, $P = 0.848$). Communal nesting in *A. scotica* seems unlikely to have arisen as a direct defence against conopid parasitism.

Frequent conopid parasitism leads to high somatic costs of mating above ground, where mating typically occurs in bees (Eickwort & Ginsberg 1980). This could have favoured intranidal mating by *A. scotica* females before they first emerged from their nests in spring. A major advantage to communal nesting would then arise from the increased access of a mother's sons to receptive females, those female offspring emerging in the same nest as her sons. Under this scenario, and assuming that incest is rare or carries little cost, every nestmate mother potentially benefits from living in the communal society.

Nest defence by nestmate *A. scotica* females could potentially reduce parasitism by the cuckoo bee *N. marshamella* as this parasite needs to enter host nests to parasitise host cells. Communal nesting may therefore be favoured in *A. scotica* through the advantages it brings in reducing cuckoo bee parasitism (Tengö 1984). Given the mode of entry of meloid triungulins into host nests, attached to host females, communal nesting in *A. scotica* is unlikely to provide a defence against these putative parasites. The relationships between communal nesting and nematode or microsporidium infection are less clear. High genetic diversity of nestmate females in social

insects has been hypothesised to enhance defence against disease microorganisms (e.g. Shykoff & Schmid-Hempel 1991). Surprisingly, then, though *A. scotica* nestmate females exhibit high relative intranidal genetic diversity (nestmate females are effectively unrelated, Paxton et al. 1996), all hosts at field site TS were infected with a microsporidium (Tab. 4). For host bees, social life may bring with it both costs as well as benefits in terms of increased or decreased rates of parasitism respectively, depending upon the lifecycle and pathogenicity of the parasite and, for parasitic microorganisms, their virulence and mode of transmission.

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Sammanfattning

Värd-parasitrelationer mellan å ena sidan det fakultativt kommunala (det vill säga ofta men inte alltid 'kollektivboende'), grävande sandbiet *Andrena scotica* (Hymenoptera: Apoidea) och å den andra tre dipterer, stekelflugan *Myopa buccata* (Conopidae), svävflugan *Bombylius major* (Bombyliidae) och blomsterflugan *Leucophora personata* (Anthomyiidae), styrks och kvantifieras genom observationer av adulta insekter vid värdbiets bomynningar, dissektion av adulta värdbin samt undersökning av värdbiets underjordiska yngelceller. Conopidparasiteringen var hög med upp till 40 % av de adulta bina per lokal innehållande en eller flera conopidlarver. De båda andra flugarterna var tillfälliga parasiter på värdens avkomma och pollenförråd. Jämförelse görs beträffande värdbonas placeringar och *Leucophora*-flugors inträngande, mellan *L. personata* och *L. obtusa* (en parasit till andra andrenid-arter). Ingen av flugarterna har sannolikt haft någon betydelse för evolutionen eller upprätthållandet av kommunaliteten i sig hos *A. scotica*. Data lämnas också om andra tänkbara parasiter och följeslagare till *A. scotica* på Öland.